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ARTÍCULO DE REVISIÓN

Ecology of Land Cover Change in Glaciated Tropical Mountains

Ecología de los cambios de cobertura del paisaje de glaciares de montañas tropicales

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Abstract

Tropical mountains contain unique biological diversity, and are subject to many consequences of global climate change, exasperated by concurrent socioeconomic shifts. Glaciers are in a negative mass balance, exposing substrates to primary succession and altering downslope wetlands and streams. A review of recent trends and future predictions suggests a likely reduction in areas of open habitat for species of high mountains due to greater woody plant cover, accompanied by land use shifts by farmers and pastoralists along the environmental gradients of tropical mountains. Research is needed on the biodiversity and ecosystem consequences of successional change, including the direct effects of retreating glaciers and the indirect consequences of combined social and ecological drivers in lower elevations. Areas in the high mountains that are protected for nature conservation or managed collectively by local communities represent opportunities for integrated research and development approaches that may provide ecological spaces for future species range shifts.

Keywords: biogeography; climate change; glaciers; land use/land cover change; tropical mountains; Andes.

Resumen

Las montañas tropicales incluyen una singular diversidad biológica sujeta a las numerosas consecuencias del cambio climático global, exacerbado por concurrentes cambios socioeconómicos. Los glaciares están en un balance negativo de su masa, promoviendo la exposición de los suelos a la colonización primaria, y alterando pantanos y riachuelos en las partes bajas. Revisiones de las tendencias actuales y predicciones sugieren que las especies de alta montaña sufrirían una reducción en las áreas de hábitats abiertos, debido al incremento en la cobertura de plantas leñosas, acompañado por los cambios en el uso del paisaje causados por agricultores y pastores a lo largo de las gradientes ambientales en las montañas tropicales. Es necesaria la investigación de las consecuencias en la biodiversidad y en los ecosistemas por causados por los cambios sucesionales, incluyendo los efectos directos del retroceso de los glaciares y las consecuencias indirectas de la acción combinada de factores sociales y ecológicos que ocurren en altitudes inferiores. Las áreas protegidas en las altas montañas usadas en la conservación de la naturaleza o manejadas colectivamente por comunidades locales representan oportunidades donde puede integrarse investigación y planes de desarrollo que podrían proveer espacios ecológicos para los futuros desplazamientos de los rangos de distribución de las especies.

Palabras claves: biogeografía; cambio climático; glaciares; uso de la tierra/cambio de cobertura; montañas tropicales; Andes.

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Introduction

The highest mountains of the tropics are affected by cold and frozen conditions, which impose climatic and edaphic biophysical constraints on the plants, animals, and ecosystem processes found there. Perennial snow occurs at high elevations along the large mountain chains and plateaus of the central Andes Mountains in the form of ice caps and mountain glaciers, especially in Peru and Bolivia. There are also tropical glaciers on isolated peaks in the northern Andes, Mesoamerica, east Africa, and New Guinea. All of these mountains and other similar ecoregions are undergoing dramatic ecological shifts owing to global change processes (MacDonald 2010, MacDougall et al. 2012, Diffenbaugh & Field 2013). The high tropical landscapes have land covers shifting due to increasing temperatures, altered precipitation regimes, and negative glacial mass balances (Bradley et al. 2009, Urrutia & Vuille 2009, Mahlstein et al. 2011). For example, a recent modeling project done by Tovar and colleagues (2013) for the tropical Andes suggests that many high elevation sites in the future will no longer support glaciers, periglacial zones, or tropical alpine vegetation. Data from resurveys of birds (Forero-Medina et al. 2011) and trees (Feeley et al. 2010) have revealed evidence of upward shifts of species distributions in forests of the mountains of southern Peru during recent decades.

Glaciated mountains will be in ecological flux as mediated through land cover changes, caused by both biophysical and socioeconomic drivers. These are montane landscapes shaped in part by legacies of past human land use, with ancient pastoralism and farming (Young 1998, 2009, Gade 1999), and also affected by current downstream human populations dependent upon glacier-fed streams for water and energy production (Bury et al. 2013, Carey et al. 2014). Assessments that include feedbacks among the social and ecological components are more likely to be able to predict complex trajectories of change, for example with thresholds or hysteresis. For example, demands for products may alter smallholder decisions, leading to land use changes that counteract or even accelerate changes due solely to climate change (Young 2013). As a result, socio-ecological feedbacks and interactions explain landscape dynamism, but may need to be examined through interdisciplinary approaches, done at multiple temporal and spatial scales, in order to clarify the processes involved. In turn, some drivers are not only slow acting, but may not easily change states, or once changed, may be put on an irreversible trajectory.

The goal of this review article is to evaluate how these processes interact to cause ecological change. This is done by identifying the major effects of glacier retreat on ecological processes, whether they act directly through changing substrate types and moisture conditions, or if they instead act indirectly by altering land use, sometimes far downslope. Landscapes change due to the interacting influences of all those drivers, including atmospheric, climatic, ecological, and socioeconomic processes. Ecological processes can be observed during primary succession on newly exposed substrates, and as shifts in the locations and characteristics of wetlands, of treelines, and in the relative abundances of woody plants.

Ecological Dynamism in Tropical Mountains

Change is caused directly by alterations in glacial mass balance, which is mediated through reduced ice cover, an initial increase in stream discharge, and the release of land for primary succession. There are also increases further away from the direct influences of the glaciers in the abundance of woody plants, perhaps due at least in part to higher carbon dioxide levels in the atmosphere. These changes will result in expansion of certain land cover types, namely pioneer plants on new substrates, and shifts in the spatial context of woody plants within landscape mosaics.

The predominant vegetation types located above altitudinal timberline and below snowline are the grasslands and shrublands of puna ecoregions found from Peru to the south, and the herbaceous or shrub páramos found in the northern Andes (Young et al. 2007), which also exist in isolated areas in Mesoamerica (Luteyn 1999). Wetlands are frequently dominated by sedges and low-growing cushion plants from genera such as *Distichia* and *Plantago*. Similar ecosystems occur at high elevations in east Africa and New Guinea (Rundel et al. 1994, Hemp 2009). The vascular plants are typically small statured, with narrow leaves or protected by thick cuticles and/or abundant hairs (Rundel et al. 1994, Körner 1999). Some dominant plants of the high mountains are large, like *Puya raimondii* of Peru and Bolivia or the *Lobelia* species of highland Kenya, and trees able to grow in exposed sites such as some of the *Polylepis* and *Buddleja* species; these tall plant life forms are growing under harsh conditions (Körner 1999, 2012).

Closer examination of the glaciated or formerly glaciated landscape mosaics will frequently reveal further ecosystem heterogeneity, associated with plants growing on substrates that vary from rocky slopes and shallow soils, to gravels, loams, and peatlands. Those mosaics can be characterized in terms of vegetation patches and habitat corridors that shift as soil moisture changes, disturbances occur, and long-term edaphic and geomorphic change takes place (e.g., Tovar et al. 2012). Landscape ecologists refer to the dominant land cover type of these mosaics as the “matrix” (Turner 2005). Figure 1 shows a glaciated landscape in the Cordillera Blanca of northern Peru, with Andean forests on the slopes, a grassland matrix, and wetlands and large erratic boulders in valley bottoms.

Species move within these changing landscapes in relationship to their habitat needs and their capacities for dispersal across the matrix. The plants that have wind-dispersed seeds and winged animals, such as birds and some insects, have the potential to arrive at most sites, with their colonization of those sites dependent on the plants encountering the necessary substrate, soil moisture, temperature regime, and solar radiation, and the animals finding appropriate habitat (e.g., Brambilla & Gobbi 2014). As a result, it can be said that the landscape mosaics interact with species adaptations through a kind of species sorting. Species with limited dispersal may take many years to colonize suitable sites. As species disperse and interact with abiotic factors and other species, they can cause ecological succession, which also has feedbacks affecting still other species. Collectively, the species populations interact in ways that can be summarized through ecosystem dynamics, their carbon stocks and fluxes, their use of water and role in hydrological transfers, and the limitations associated with nitrogen availability in its various forms.

High tropical mountains support biologically diverse ecosystems, with a year round growing season for plants and microbes, and with cold extremes at night, rather than during a cold winter season, with many implications for biodiversity patterns (Rundel et al. 1994, Körner 1999) and ecosystem processes (Ponette-

Figure 1. Glaciated landscape in the Cordillera Blanca of northern Peru.

González et al. 2014). Edaphic specialists are found on the sites frequently frozen and refrozen due to needle ice formation (Cano et al. 2011). Additional place-to-place differences are related to the topography that produces steep environmental gradients and causes turnovers in biota at major biogeographical barriers (Vuilleumier & Monasterio 1986, Young et al. 2002, Young et al. 2007). Also, there is a long history of human use of many montane landscapes (Young 2009). Many areas have direct and ongoing human impacts, through burning, grazing of domesticated livestock, mining, planting trees, or trekking. Other social and economic changes affect land use goals, for example, whether landscapes are utilized for nature conservation, housing, energy production, or grazing.

Globally induced biophysical changes will tend to shift ecosystems upslope with temperature increases. However, human land use may only partly be able to adaptively move along with those changes because social institutions that govern access to natural resources and land tenure will not be able to change along those same environmental gradients (e.g., Hobbs et al. 2008). Human institutional, legal, and political change can be much slower to manifest in ecological landscapes than alterations in distributions of plants and animals. Predictions of future landscape dynamism in tropical mountains can be made by contrasting glaciated landscapes to those that have already lost their glaciers, due to having lower mountain elevations and more exposure to dry conditions. Postigo et al. (2008) used Landsat satellite imagery to measure the land cover change associated with the deglaciation of part of high elevation Huancavelica in central Peru from 1990 to 2000. The landscape mosaics shifted from matrices of mountain glaciers and puna/tropical alpine vegetation types, to landscapes with no glaciers, larger lakes, and growing wetlands.

In other words, change in high tropical mountains is only in part driven by climate shifts affecting snow, ice, and glaciers. Human-caused influences can reach snowline, and many lower elevation areas have land cover types created by people, including entire landscape matrices dedicated to crops, housing, roads, or tree plantations. The expectation for the biogeography of the future in these mountains is not simple upslope movements, given that species must disperse and colonize in and across utilized landscapes. Plants, animals, and land-use systems will appear in places once covered by snow and ice with deglaciation. However, in other montane areas, species and land use may instead shift along gradients of humidity or disturbance, in relation to species adaptations for dispersal and colonization, and the adaptability of human populations and institutions.

Perennial Snow and Ice

During the past three decades, the glaciers of the tropics have had negative mass balances, with retreating glaciers (Thompson et al. 2006, Radic & Hock, 2011; Rabatel et al. 2013). As examples illustrating this global phenomenon, Klein and Kincaid (2006) showed dramatic glacier loss in Irian Jaya, Indonesia; Thompson et al. (2009) found that 85% of ice cover of Mt. Kilimanjaro present in 1912 is now gone, with especially rapid loss of area and volume of ice since 1989; Delgado Granados et al. (2007) measured glacier loss in a Mexico volcano top due

Figure 2. Visitors to the receding Pastoruri Glacier in 2014 in the Cordillera Blanca of Peru. They are on a day trip with a climate change motif.

to both climate warming and volcanism; Ramírez et al. (2001) documented the disappearance of small glaciers in Bolivia; Jomelli et al. (2011) examined glacier retreat over the Holocene for the Cordillera Real of Bolivia, with especially rapid loss in the last century and linked to warmer atmospheric and Pacific Ocean temperatures; López-Moreno et al. (2014) reported a 56% decrease in glacial cover and an increase in size of glacial lakes in central Peru; and Ceballos et al. (2006) described how important scale-and edge-related effects were acting on the cryosphere of Colombia, making the smaller glaciers there melt especially quickly.

Tropical glaciers have an east-west asymmetry (Young 1989, Evans & Cox 2005) because moist air masses tend to come in an easterly direction, bringing moisture from the humid lowlands. Gravity moves water and ice downhill, creating tension crevasses on the surface of mountain glaciers, and bedrock and fluvial erosion below (Benn & Evans 2010, Käser & Osmaston 2002). The erosive and depositional processes connect to a variety of ecosystem responses, e.g. Fountain et al. (2012). There are seasonal shifts in precipitation caused by movements of the Intertropical Convergence Zone, in some places also with monsoonal circulations (Hastenrath 1991, Metcalfe & Nash 2012). The slope exposures that are located on the leeward side of mountains have smaller glaciers, as snow input is less (Mark & Seltzer 2005); glaciers found in drier environments are located higher in elevation (Hastenrath 2009). There are also catastrophic changes associated with the melting glaciers, as snow avalanches can be common, and large ones may burst terminal moraines of glacial lakes causing downstream flooding (Carey 2005, 2010, Carey et al. 2012). Over previous centuries, those kinds of mass movements filled valley bottoms with glacial tills and colluvium, creating low gradient slopes and relatively flat bottomed valleys (Fig. 1).

Ecological landscapes near glaciers change as water stored in the form of ice becomes available to the environment. In addition, the rock and dust particles once suspended within the ice are deposited on the ground surface creating moraines. The rate of retreat is a function of how much melting and sublimation takes place, with the input of new snow through precipitation less than the mass of what is being converted into liquid or gaseous water. The resulting deglaciated landscape consists of a landscape matrix transformed from the cryosphere into one dominated by rocks, with moraines and tills left behind, with scattered patches of remnant ice or of colonizing plants, and corridors formed by glacial streams and developing peatlands. The nival landscape is reshaped into mounds of rocky substrates of different sizes, dissected by dozens of small streams and ponds. Figure 2 shows such as landscape, in the vicinity of what remains of the Pastoruri Glacier in the Cordillera Blanca of northern Peru.

Primary Succession after Glacier Retreat

Ecosystem recovery when soil does not exist is called primary succession (Walker and del Moral 2003). Soils develop as plant, animal, fungal, and microbial species colonize the available substrate, in this case, gravels and silts exposed by glacial retreat.

Figure 3. Wetlands and ponds in the valley bottoms of the Cordillera Blanca of Peru.

Observations in southern Peru have been made on primary succession near the Quelccaya Ice Cap and on the Vilcanota Cordillera. Freeman et al. (2009) found that saturated periglacial soils were dominated by chytrid fungi (Chytridiocycota), which presumably carry out decomposition. Those fungal communities are similar to those found in other similar sites worldwide, and all evidence points to the importance of fungi, and also algae and microbes, for primary succession following deglaciation (Freeman et al. 2009, Schmidt et al. 2012, 2014).

Those fungal, algal, and microbial organisms begin nitrogen cycling, photosynthesis, and biomass formation such that a living crust can develop on the soil within about a decade. Vascular plants only become conspicuous later. For example, Seimon et al. (2007) describe landscape change here, with new ponds and streams in deglaciated areas and with vascular plant species colonizing up to around 5500 m. Schmidt et al. (2009) measured temperatures in periglacial soils at 5400 m and at 5 cm depth that varied from 27 °C in the day and -12 °C at night. Nitrogen cycling was associated with fixation by *Nitrospira* nitrifiers and oxidation by Betaproteobaceria, while available phosphorus was low enough to limit microbial growth (Schmidt et al. 2011).

There are microsites where primary succession may be speeded by the addition of organic matter, which would quicken soil development. For example, poorly drained areas have wetland vegetation, which begins to develop organic soils and peatlands. The retreat of the Quelccaya Ice Cap exposed well-preserved plant materials 5200 to 6300 years old (Thompson et al. 2006, 2013), which will also become part of the soil as decomposition processes begin to function.

Aquatic and Wetland Ecosystems

Many climate change consequences below snowline are associated with increased water flows from the initial melting process, some of which may move through the valley system catastrophically. However, over time, total annual stream discharge will tend to drop after reaching a peak, perhaps several decades later (Baraer et al. 2012), as has been recorded for most of the watersheds of the Cordillera Blanca (Bury et al. 2013). Because dry season discharge is maintained by groundwater flows and inputs from glacial meltwaters in seasonal tropical climates, streams not influenced by the glaciers will have low discharges or even be intermittent during dry seasons. Thus, glacier retreat removes an environmental subsidy provided by this seasonal hydrological input. The wetlands, streams, and ponds tend to be found in lower topographic positions, found in valley bottoms and receiving hydrologic inputs from precipitation, groundwater, and surface water flows (Fig. 3).

Over decades to centuries following deglaciation, proglacial lakes may completely fill with organic sediments. This leaves a sedimentary record of a switch from inorganic sediments that characterize glacial erosive processes to those resulting from biotic processes in the watershed (Rodbell et al. 2008, Stansell et al. 2013). The organic sediments document several kinds of ecosystem succession, with an autogenic process that ends with lakes filling in and transforming into seasonal or permanent wetlands, with their respective species. However, there is also ongoing terrestrial succession, providing materials entering the lakes that come from erosion and runoff as vegetation covers landscape positions once occupied by glaciers.

Proglacial lakes and wetlands, adjacent to a glacier, grow in size with the initial pulse of water from the retreating glacier. Lipton (2008) measured increases in size of proglacial lakes and valley-bottom wetlands in Landsat imagery from 1989 to 2001 in the Cordillera Blanca. Perhaps due to less water moving through the system some years later, Bury et al. (2013) found that for the Quilcayhuanca valley, the wetlands showed a decrease of 17% in area from 2000 to 2011 and were more fragmented, suggesting that peak water from glacier retreat had already moved through. Hydrological modeling can be used to evaluate likely future change in these ecosystems. For example, Buytaert and Beven (2011) used several kinds of models to show how lakes and wetlands can augment dry season flows. There are also implications for ecosystem functions and services (Buytaert et al. 2011), as carbon stored in the organic matter of wetland peats was created by photosynthesis decades or centuries previously. Lower or fluctuating water levels will add carbon dioxide to the atmospheric as decomposition rates increase.

These kinds of landscape changes will also have implications for the assembly of plant and animal species that require wetland and aquatic habitats. For example, in the Vilcanota Cordillera, Seimon et al. (2007) reported that climate change caused the exposure of an ice-free corridor that allowed species to move across the topographic divide, while also expanding aquatic environments in the form of streams and ponds. They were able to document upward altitudinal shifts of three frog species, tracking the habitat changes. Worryingly, they also found upward shifts in the chytrid fungus that infects and kills many frog species (Collin & Crump 2009).

The ecological development of streams following deglaciation has been studied by researchers who found a relatively high diversity of aquatic invertebrates, which also changes as a function of distance from direct glacier influences. For example, Kuhn et al. (2011) measured downstream changes in stream temperature, substrate type, and channel stability as related to distance from a glacial margin in highland Ecuador. They were using space as a substitute for successional time: a chronosequence approach. The physical changes along the reach of the channel and the chemical changes of the water all caused shifts in the composition, density, and species richness of aquatic invertebrates. Similar sampling led Boyero et al. (2012) to state that tropical stream detritivores are particularly at risk from climate changes, given their high beta diversity, with much place-to-place uniqueness in the species present. Jacobsen et al. (2012) show potential losses of both alpha and beta diversity with glacial retreat differentially affecting specialist species. Loayza-Muro et al. (2010) report dramatic changes in the aquatic invertebrates caused by the new bedrock exposed by glacial retreat changing water chemistry. Because hydrological connectivity links these kinds of changes to further downstream shifts in stream ecology, it is possible that deglaciation will affect whole river basins.

Dynamics of Woody Plants

Increasing atmospheric carbon dioxide may favor plants with C3 photosynthesis, making them more efficient in terms of water use and hence potentially shifting grasslands to having an increased woody plant presence (Polley et al. 1994, Morgan et al. 2007, Higgins & Scheiter 2012). Globally, in recent decades, there are often signs of increased shrubland areas, in some cases likely due also to land use change, release from overgrazing, and altered fire regimes (Eldridge et al. 2012). Naito and Cairns (2011) think that increased shrub dominance in the arctic is caused by the warming of temperatures there. Some encroachment is also due to the introduction of exotic woody species that are invasive (Rundel et al. 2014).

In tropical mountains, increases in woody plant coverage were reported based on Landsat satellite images by Kintz et al. (2006) and Lipton (2008), with studies of seedling establishment in the timberline zone by Rehm and Feeley (2013), and in mapping done using MODIS data by Aide et al. (2013), who report many dry and steep areas with expanding or regrowing forests or shrublands. These changes are those expected globally, and are also those found in the modeling done by Tovar et al. (2013), who predict shifts in ecological zones, with more area in the tropical Andes with montane shrublands and seasonally dry forest. Gosling et al. (2009) use paleoecological information on *Polylepis* species to suggest that predictions for warmer and drier climates in the Andes of the future would limit places where those species could survive.

However, woody plant dynamics are spatially variable. For example, Byers (2000) found relatively stable margins for forest edges in the Cordillera Blanca; Coblentz and Kintz (2008) documented relatively little change in forest patches in southern Ecuador in terms of forest edges and hence patch location, size, and shape; and the forest patches studied by Jameson and Ramsay (2007) in southern Peru were similar in size over 50 years, although they became less dense. Many of the studies in the Andes implicate a complicating role of land use, with loss of forest due to burning (Cierjacks et al. 2008), and with less habitat available for specialist forest species (Lloyd 2008, Gareca et al. 2010, Tinoco et al. 2013). Hensen and colleagues (2012) showed that topographic barriers and human-caused habitat fragmentation are both constraining the genetic diversity of *Polylepis incana* in Ecuador.

Treeline limits may also be expected to shift, upward when controlled by temperature, but perhaps downward if the tree species are limited instead by moisture regimes or by human land use (Young 1993, Hemp 2009, Holtmeier 2009, Malanson et al. 2011, Körner 2012). Young and León (2007) noted that tropical timberline landscape mosaics revealed upward shifts of forest edges and higher forest patches, but also in some sites timberline was being lowered. Forest limits include the moderating influence of the higher relative humidity found within interior forest. In other areas, there may be increased shrub colonization into grasslands, which increases woody cover. The research of Bader and Ruijten (2008) in Ecuador points to additional site-to-site heterogeneity due to the combined effects of elevation, topographic position, and slope aspect. All of these shifts have implications for the associated carbon dynamics (Zimmermann et al. 2010), and hence the ecosystem services provided (Balthazar et al. 2015).

Anthropogenic Landscapes

Humans create new land cover patches by inserting pastures, agricultural fields, and mines into tropical alpine landscapes. Land use alters ecosystem dynamics and landscape mosaics by introducing novel cover types, by increasing some cover types while decreasing others, and by changing the shapes, sizes, and locations of patches and corridors. Large-scale drivers of change may alter the type of matrix. All of these kinds of land-use related changes can be found in the high tropical mountains of the world (Spehn et al. 2006). The tropical Andes in particular have a long history of human-caused alterations in land cover (Young 1997, 1998, 2009), with ancient deforestation and its large fauna mostly extirpated and only surviving in nature reserves.

Many tropical mountains have shrubland matrices where native forests are restricted to isolated patches (Young & Keating 2001), exotic tree plantations are found, and agricultural fields form patches of crops and fallow (Young 2009). The need for wood requires harvesting from remaining forest patches (Young 1993). In other areas, the establishment of tree plantings has increased the production of wood products, although often the species of pines and eucalypts planted do not act to create habitats useful for native species. Trees transpire more than herbaceous plants, so tree plantings use more water, which result in reduced stream flow (Bruijnzeel 2004, Ponette-González et al. 2014). Harden et al. (2013), for example, showed afforestation left less water available in sites in highland Ecuador.

Probably the biggest influence on land cover from human land use comes from the combined and persistent actions of thousands of smallholders, who manage multiple fields and pastures across a range of environmental gradients (Zimmerer 1999, Mayer 2002). Some of the influences on land use in tropical mountains originate as distant or global socioeconomic processes; that is, they are telecoupled (Liu et al. 2013). For example, the international values of mineral resources affect the locations of mines (Bebbington & Bury 2013), and hence the impacts they may have on land cover and on water resources. There are continuing social and health concerns associated with those activities, including legacies of past exploitation (Postigo et al. 2013).

Glacial retreat provides new spaces for ecological change, while also creating sites that can be used for pasture or for the planting of high Andean crops. A former nival landscape would become a successional landscape with primary succession, but also support grazing livestock and agricultural fields. In the tropical Andes, those new spaces would typically be managed communally, with access to pasture or for farming distributed among kinship groups or through governance of nearby municipalities (Young & Lipton 2006). Burning and the organized rotation of grazing are common rangeland management approaches, which means even very high elevation sites may receive some degree of human influence on biodiversity patterns and ecosystem processes. The high elevation wetlands, for example, can be transformed into potato fields by farmers (Zimmerer 1991), so they may be targeted for conversion for agriculture. Postigo (2012) reports on formerly exclusive pastoralists adjacent to the Quelccaya Ice Cap who have recently adapted their land use to include the planting of crops on lands that before had only been used for grazing.

Changes in the tropical cryosphere have many implications for people living downslope, from increased natural hazards, to decreased water quality and supply. There are also expectations of complex ecosystem shifts in the mountains (e.g., Tovar et al. 2013). For example, dry valleys have shrublands and relict patches of native forest, so future change might be to increase shrubland density in those intermontane locations. There would then be feedbacks through land use as peoples' options for planting or grazing change. As their livelihoods are changed, their effect on land cover would be modified (Young 2008, 2013), with further repercussions for landscapes near and within the cryosphere. By examining these interactive systems, it would be possible to decipher the effects of climate change, the aspects due to human impacts, and finally the effects of the interactions of all of the drivers of change.

Public land designation for nature conservation is an important land use. The highest elevations had touristic and scenic values, leading to the establishment of national parks or their equivalents (e.g., Rodriguez & Young 2000). In practice, often land use from adjacent communities has continued, leading to mixed land use of rangeland and nature conservation, which may generate incompatibilities and conflicts (Young & Lipton 2006). Climate change creates dramatic challenges to protected areas, bringing land cover shifts into the area, accompanied by new anthropogenic threats and impacts (Monzón et al. 2011). There may be increased conflicts between the protected areas and local people who find their livelihood strategies limited. Often protected areas receive credit for the ecosystem and environmental services they provide, which may lessen with climate change (Jackson et al. 2009, Buytaert et al. 2011).

The world has become more urban, e.g. Álvarez-Berríos et al. (2013), and this includes areas in high tropical mountains affected directly by the growth of cities, or indirectly as rural abandonment has taken place. Land use can be intensified with larger markets available to sell products, leading to the establishment of more tree plantations and more intensive crop production systems (Aide et al. 2013). In other situations, land use may become less intense as people move to the city, although it may then become more extensive, with larger areas kept in rangeland to provide meat and fiber to the city. Needs for electricity may divert water resources to hydroelectric facilities, including those powered by water provided by glaciers (Bury et al. 2013, Carey et al. 2014). All these economic and demographic trends would increase extraction of natural resources, including water, minerals from the subsurface (Bebbington & Bury 2013), forest products (e.g., Young 1993, 1997, Balthazar et al. 2015), and the need for lands for food production (Mark et al. 2010).

Conclusions

There will be hotspots of change, especially near glaciers where climate-caused alterations in land cover and ecosystem processes has been the greatest in the past decades in tropical mountains. However, the increase in areas with woody plants will likely continue, possibly even threatening the future existence over the next century of habitat types dominated by herbaceous plants, over broad expanses of tropical mountains. Other places will need to house urban populations or produce commodities for world markets.

Mora et al. (2013) suggest that the tropical countries will be among the first affected by climate change. Research is needed to address the concerns raised. Measuring rates of ecological change, for example by monitoring land cover change (Haller 2012), ecological succession (Schmidt et al. 2008), changing species distributions (Feeley & Silman 2010), soil nutrients and moisture (Farley 2007), soil bacteria (Evans & Wallenstein 2014), ecological thresholds (Bush et al. 2010), or shifting landscape mosaics (Kintz et al. 2006), will all be important means to provide early notice of where and when important landscape dynamics are taking place. Research from the Alps suggests that the high-mountain plant species are at particular risk (Dullinger et al. 2012); the findings of Williams et al. (2007) illustrate the degree to which novel climate types and species assemblages are to be expected in tropical mountains.

There are also temporal mismatches to address in this kind of research. For example, important soil properties may develop over decades to centuries, while nitrogen stocks that affect plant growth may change in weeks, and soil moisture and surface temperatures vary daily or even hourly. Farmers and pastoralists must somehow assess these biophysical conditions and may modify their decisions concerning planting schedules, crop choices, and herd sizes from one season to another, or may adapt their production systems to the new conditions. The changes affecting landscapes also have ecosystem implications, including for environmental services that are directly or indirectly useful to people. The changes occurring in the high tropics thus have numerous economic and political consequences

Watershed research approaches can link glacial and ecological change to resulting stream discharges and water resource availability (Buytaert & Beven 2011, Carey et al. 2014, Ponette-González et al. 2014). Indeed the risk posed by natural hazards also has a watershed dimension, as glacial lakes may catastrophically affect people and their livelihoods downslope (Carey 2010). More subtle land cover changes can be evaluated through socio-ecological interactions that connect to economic and political decisions taking place elsewhere (Mark et al. 2010, Valdivia et al. 2010, Bury et al. 2013, Huber et al. 2013).

The ice-capped archipelagos of tropical mountains are sites of high speciation rates over evolutionary time (Luebert & Weigend 2014, Sklenár et al. 2014), for example, for Andean plants such as the lupines (*Lupinus*) (Hughes & Eastwood 2006) and birds such as tanagers (Sedan & Burns 2010). Over millions of years, these processes explain the adaptations of the species and the characteristics of the biodiversity hot spots in the tropical Andes, the highlands of Mesoamerica, and the mountains of Africa and New Guinea (Myers et al. 2000, Olson et al. 2001). Mutke et al. (2014), for example, found much recent speciation associated with disturbances and habitat availability in the mountains of northern Peru. However, that evolutionary capacity for speciation and adaptation probably cannot match the rates and kinds of rather different socio-ecological processes happening in today's tropical landscapes and in those of the future. Extinction can and does happen in ecological time, meaning that potential habitat loss must be addressed now, developing analyses of landscape connectivity that will permit future biogeographical shifts, while also considering the livelihoods of the people affected. Public lands protected for biodiversity in tropical mountains are in areas considered to be of little value for settlements and farming; other high elevation sites are managed as common pool resource areas by local communities. These sites represent opportunities for integrated approaches to socio-ecological change, as adjusted to land use goals and as calibrated to provide opportunities for future species range shifts.

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Literature cited

Aide T.M., M.L. Clark, H.R. Grau, D. López-Carr, M.A. Levy, D. Redo, M. Bonilla-Moheno, G. Riner, M.J. Andrade-Núez, & M. Mu-iz. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45:262-271. http://dx.doi.org/10.1111/j.1744-7429.2012.00908.x

Álvarez-Berríos, N.L., I.K. Parés-Ramos, & T.M. Aide. 2013. Contrasting patterns of urban expansion in Colombia, Ecuador, Peru, and Bolivia between 1992 and 2009. Ambio 42:29-40. http://dx.doi.org/10.1007/s13280-012-0344-8

Bader, M.Y., & J.J.A. Ruijten. 2008. A topography-based model of forest cover at the alpine tree line in the tropical Andes. Journal of Biogeography 35:711-723. http://dx.doi.org/10.1111/j.1365-2699.2007.01818.x

Baraer, M., B.G. Mark, J.M. McKenzie, T. Condom, J. Bury, K-.I. Huh, C. Portocarrero, J. Gómez, & S. Rathay. 2012. Glacier recession and water resources in Peru's Cordillera Blanca. Journal of Glaciology 58:134-150.http://dx.doi.org/10.3189/2012JoG11J186

Balthazar, V., V. Vanacker, A. Molina, & E.F. Lambin. 2015. Impacts of forest cover change on ecosystem services in high Andean mountains. Ecological Indicators 48:63-75. http://dx.doi.org/10.1016/j.ecolind.2014.07.043

Bebbington, A.J. & J. T. Bury, eds. 2013. Subterranean Struggles: New Geographies of Extractive Industries in Latin America. University of Texas Press, Austin.

Benn, D.I. & D.J.A. Evans. 2010. Glaciers and Glaciation, 2 edn. London, Hodder Arnold, London.

Boyero, L., R.G. Pearson, D. Dudgeon, V. Ferreira, et al. 2012. Global patterns of stream detritivore distribution: Implications for biodiversity loss in changing climates. Global Ecology and Biogeography 21:134-141. http://dx.doi.org/10.1111/j.1466-8238.2011.00673.x

Bradley, R.S., F.T. Keimig, H.F. Diaz, & D.R. Hardy. 2009. Recent changes in freezing level heights in the tropics with implications for the deglacierization of high mountain regions. Geophysical Research Letters 36, L17701. http://dx.doi.org/10.1029/2009GL037712

Brambilla, M., & M. Gobbi. 2014. A century of chasing the ice: Delayed colonization of ice-free sites by ground beetles along glacier forelands in the Alps. Ecography 37:33-42. http://dx.doi.org/10.1111/j.1600-0587.2013.00263.x

Bruijnzeel, L.A. 2004. Hydrological functions of tropical forests: Not seeing the soil for the trees? Agriculture Ecosystems & Environment 104:185–228. http://dx.doi.org/10.1016/j.agee.2004.01.015

Bury, J., B.G. Mark, M. Carey, K.R. Young, J. McKenzie, M. Baraer, A. French, & M.H. Polk. 2013. New geographies of water and climate change in Peru: Coupled natural and social transformations in the Santa River watershed. Annals of the Association of American Geographers 103:363-e74. http://dx.doi.org/10.1080/00045608.2013.754665

Bush, M.B., J.A. Hanselman, & W.D. Gosling. 2010. Nonlinear climate change and Andean feedbacks: An imminent turning point? Global Change Biology 16:3223-3232. http://dx.doi.org/10.1111/j.1365-2486.2010.02203.x

Buytaert, W., & K. Beven. 2011. Models as multiple working hypotheses: Hydrological simulation of tropical alpine wetlands. Hydrological Processes 25:1784-1799. http://dx.doi.org/10.1002/hyp.7936

Buytaert, W., F. Cuesta-Camacho, & C. Tobón. 2011. Potential impacts of climate change on the environmental services of humid tropical alpine regions. Global Ecology and Biogeography 20:19-33. http://dx.doi.org/10.1111/j.1466-8238.2010.00585.x

Byers, A.C. 2000. Contemporary landscape change in the Huascarán National Park and buffer zone, Cordillera Blanca, Peru. Mountain Research and Development 20:52-63. http://dx.doi.org/10.1659/0276-4741(2000)020[0052:CLCITH]2.0.CO;2

Cano, A., A. Delgado, W. Mendoza, et al. 2011. Flora y vegetación de suelos crioturbados y hábitats asociados en los alrededores del abra Apacheta, Ayacucho-Huancavelica (Perú). Revista peruana de biología 18:169-178. http://dx.doi.org/10.15381/rpb.v18i2.224

Carey, M. 2005. Living and dying with glaciers: people's historical vulnerability to avalanches and outburst floods in Peru. Global and Planetary Change 47:122-134. http://dx.doi.org/10.1016/j.gloplacha.2004.10.007

Carey, M. 2010. In the Shadow of Melting Glaciers: Climate Change and Andean Society. Oxford University Press, Oxford. http://dx.doi.org/10.1093/acprof:oso/9780195396065.001.0001

Carey, M., M. Baraer, B.G. Mark, A. French, J. Bury, K.R. Young, & J. M. McKenzie. 2014. Toward hydro-social modeling: Merging human variables and the social sciences with climate-glacier runoff models (Santa River, Peru). Journal of Hydrology 518:60-70. http://dx.doi.org/10.1016/j.jhydrol.2013.11.006

Carey, M., C. Huggel, J. Bury, C. Portocarrero, & W. Haeberli. 2012 An integrated socio-environmental framework for glacier hazard management and climate change adaptation: Lessons from Lake 513, Cordillera Blanca, Peru. Climatic Change 112:733-767. http://dx.doi.org/10.1007/s10584-011-0249-8

Ceballos, J.L., C. Euscátegui, J. Ramírez, M. Ca-on, C. Huggel, W. Haeberli, & H. Machguth. 2006. Fast shrinkage of tropical glacier in Colombia. Annals of Glaciology 43:194-201. http://dx.doi.org/10.3189/172756406781812429

Cierjacks, A., S. Salgado, K. Wesche, & I. Hensen. 2008. Post-fire population dynamics of two tree species in high-altitude Polylepis forests of central Ecuador. Biotropica 40:176-182. http://dx.doi.org/10.1111/j.1744-7429.2007.00361.x

Coblentz, D., & P.L. Kintz. 2008. Topographic controls on the distribution of tree islands in the high Andes of south-western Ecuador. Journal of Biogeography 35:2026-2038. http://dx.doi.org/10.1111/j.1365-2699.2008.01956.x

Collins, J.P., & M. L. Crump. 2009. Extinction in our Times: Global Amphibian Declines. Oxford University Press, Oxford.

Delgado Granados, H., P.J. Miranda, C. Huggel, S. Ortega del Valle, & M.A. Alatorre Ibargüengoitia. 2007. Chronicle of a death foretold: Extinction of the small-size tropical glaciers of Popocatépetl volcano (Mexico). Global and Planetary Change 56:13-22. http://dx.doi.org/10.1016/j.gloplacha.2006.07.010

Diffenbaugh, N.S., & C.B. Field. 2013. Changes in ecologically critical terrestrial climate conditions. Science 341:486-492. http://dx.doi.org/10.1126/science.1237123

Dullinger, S., A. Gattringer, W. Thuiller, D. Moser, et al. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change 2:619-622. http://dx.doi.org/10.1038/nclimate1514

Eldridge, D.J., M.A. Bowker, F.T. Maestre, E. Roger, J.F. Reynolds, & W.G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. Ecology Letters 14:709-722. http://dx.doi.org/10.1111/j.1461-0248.2011.01630.x

Evans, I.S., & N.J. Cox. 2005. Global variations of local asymmetry in glacier altitude: Separation of north-south and east-west components. Journal of Glaciology 51:469-482. http://dx.doi.org/10.3189/172756505781829205

Evans, S.E., & M.D. Wallenstein. 2014. Climate change alters ecological strategies of soil bacteria. Ecology Letters 17:155-164. http://dx.doi.org/10.1111/ele.12206

Farley, K.A. 2007. Grasslands to tree plantations: Forest transition in the Andes of Ecuador. Annals of the Association of American Geographers 97:755-771. http://dx.doi.org/10.1111/j.1467-8306.2007.00581.x

Feeley, K.J., & M.R. Silman. 2010. Modelling the responses of Andean and Amazonian plant species to climate change: The effects of georeferencing errors and the importance of data filtering. Journal of Biogeography 37:733-740. http://dx.doi.org/10.1111/j.1365-2699.2009.02240.x

Feeley, K.J., M.R. Silman, M.B. Bush, et al. 2010. Upslope migration of Andean trees. Journal of Biogeography 38:783-791. http://dx.doi.org/10.1111/j.1365-2699.2010.02444.x

Forero-Medina, G., J. Terborgh, S.J. Socolar y S.L. Pimm. 2011. Elevational Ranges of Birds on a Tropical Montane Gradient Lag behind Warming Temperatures. PLoS ONE 6 (12): e28535. http://dx.doi.org/10.1371/journal.pone.0028535

Fountain, A.G., J.L. Campbell, E.A.G. Schuur, S.E. Stammerjohn, M.W. Williams, & H.W. Ducklow. 2012. The disappearing cryosphere: Impacts and ecosystem responses to rapid cryosphere loss. Bioscience 62:405-415. http://dx.doi.org/10.1525/bio.2012.62.4.11

Freeman, K.R., A.P. Martin, D. Karki, R.C. Lynch, M.S. Mitter, A.F. Meyer, J.E. Longcore, D.R. Simmons, & S.K. Schmidt. 2009. Evidence that chytrids dominate fungal communities in high-elevation soils. Proceedings of the National Academy of Science 106:18315-18320. http://dx.doi.org/10.1073/pnas.0907303106

Gade, D.W. 1999. Nature and Culture in the Andes. University of Wisconsin Press, Madison.

Gareca, E.E., M. Hermy, J. Fjeldså, & O. Honnay. 2010. Polylepis woodland remnants as biodiversity islands in the Bolivian high Andes. Biodiversity and Conservation 19:3327-3346. http://dx.doi.org/10.1007/s10531-010-9895-9

Gosling, W.D., J.A. Hanselman, C. Knox, B.G. Valencia, & M.B. Bush. 2009. Long-term drivers of change in Polylepis woodland distribution in the central Andes. Journal of Vegetation Science 20:1041-1052. http://dx.doi.org/10.1111/j.1654-1103.2009.01102.x

Haller, A. 2012. Vivid valleys, pallid peaks? Hypsometric variations and rural-urban land change in the central Peruvian Andes. Applied Geography 35:439-447. http://dx.doi.org/10.1016/j.apgeog.2012.09.009

Harden, C.P., J. Hartsig, K.A. Farley, J. Lee, & L.L. Bremer. 2013. Effects of land-use change on water in Andean páramo grassland soils. Annals of the Association of American Geographers 103:375-384. http://dx.doi.org/10.1080/00045608.2013.754655

Hastenrath, S. 1991. Climate Dynamics of the Tropics. Springer-Kluwer, Netherlands. http://dx.doi.org/10.1007/978-94-011-3156-8

Hastenrath, S. 2009. Past glaciation in the tropics. Quaternary Science Reviews 28:790-798. http://dx.doi.org/10.1016/j.quascirev.2008.12.004

Hemp, A. 2009. Climate change and its impact on the forests of Kilimanjaro. African Journal of Ecology 47, suppl. 1:3-10. http://dx.doi.org/10.1111/j.1365-2028.2008.01043.x

Hensen, I., A. Cierjacks, H. Hirsch, M. Kessler, K. Romoleroux, D. Renison, & K. Wesche. 2012. Historic and recent fragmentation coupled with altitude affect the genetic population structure of one of the world's highest tropical tree line species. Global Ecology and Biogeography 21:455-464. http://dx.doi.org/10.1111/j.1466-8238.2011.00691.x

Higgins, S.I., & S. Scheiter. 2012. Atmospheric CO2 forces abrupt vegetation shifts locally, but not globally. Nature 488:209-213. http://dx.doi.org/10.1038/nature11238

Hobbs, N.T., K.A. Galvin, C.J. Stokes, J.M. Lackett, A.J. Ash, R.B. Boone, R.S. Reid, & P.K. Thornton. 2008. Fragmentation of rangelands: Implications for humans, animals, and landscapes. Global Environmental Change 18:776-785. http://dx.doi.org/10.1016/j.gloenvcha.2008.07.011

Holtmeier, F.-K. 2009. Mountain Timberlines-Ecology, Patchiness, and Dynamics. Advances in Global Change Research, 36. Springer, Dordrecht.

Huber, R., A. Rigling, P. Bebi, et al. 2013. Sustainable land use in mountain regions under global change: Synthesis across scales and disciplines. Ecology and Society 18(3): 36. htpp://dxdoi.org/10.5751/ES-05499-180336

Hughes, C., & R. Eastwood. 2006. Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. Proceedings of the National Academy of Science 103:10334-10339. http://dx.doi.org/10.1073/pnas.0601928103

Jackson, R.B., E.G. Jobbágy, & M.D. Nosetto. 2009. Ecohydrology in a human-dominated landscape. Ecohydrology 2:383-389. http://dx.doi.org/10.1002/eco.81

Jacobsen, D., A.M. Milner, L.E. Brown, & O. Dangles. 2012. Biodiversity under threat in glacier-fed river systems. Nature Climate Change 2:361-364. http://dx.doi.org/10.1038/nclimate1435

Jameson, J.S., & P.M. Ramsay. 2007. Changes in high-altitude Polylepis forest cover and quality in the Cordillera de Vilcanota, Peru, 1956-2005. Biological Conservation 138:38-46. http://dx.doi.org/10.1016/j.biocon.2007.04.008

Jomelli, V., M. Khodri, V. Favier, D. Brunstein, et al. 2011. Irregular tropical glacier retreat over the Holocene epoch driven by progressive warming. Nature 474:196-199. http://dx.doi.org/10.1038/nature10150

Käser, G., & H. Osmaston. 2002. Tropical Glaciers. Cambridge University Press, Cambridge.

Kintz, D.B., K.R. Young, & K.A. Crews-Meyer. 2006. Implications of land use/land cover change in the buffer zone of a national park in the tropical Andes. Environmental Management 38:238-252. http://dx.doi.org/10.1007/s00267-005-0147-9

Klein, A.G., & J.L. Kincaid. 2006. Retreat of glaciers on Puncak Jaya, Irian Jaya, determined from 2000 and 2002 IKONOS satellite images. Journal of Glaciology 52:65-79. http://dx.doi.org/10.3189/172756506781828818

Körner, C. 1999. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Springer, Berlin. http://dx.doi.org/10.1007/978-3-642-98018-3

Körner, C. 2012. Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits. Springer, Basel. http://dx.doi.org/10.1007/978-3-0348-0396-0

Kuhn, J., P. Andino, R. Calvez, R. Expinosa, L. Hamerlik, S. Vie, O. Dangles, & D. Jacobsen. 2011. Spatial variability in macroinvertebrate assemblages along and among neighbouring equatorial glacier-fed streams. Freshwater Biology 56:2226-2244. http://dx.doi.org/10.1111/j.1365-2427.2011.02648.x

Lipton, J.K. 2008. Human Dimensions of Conservation, Land Use, and Climate Change in Huascaran National Park, Peru. Doctor of Philosophy Dissertation. University of Texas, Austin.

Liu, J., V. Hull, M. Batistella, et al. 2013. Framing sustainability in a telecoupled world. Ecology and Society 18: 92; 26. http://dx.doio.org/10.5751/ES-05873-180226

Lloyd, H. 2008. Foraging ecology of high Andean insectivorous birds in remnant Polylepis forest patches. The Wilson Journal of Ornithology 120:531-544. http://dx.doi.org/10.1676/07-059.1

Loayza-Muro, R.A., R. Elías-Letts, J.K. Marticorena-Ruíz, E.J. Palomino, J.F. Duivenvoorden, M.H.S. Kraak, & W. Admiraal. 2010. Metal-induced shifts in benthic macroinvertebrate community composition in Andean high altitude streams. Environmental Toxicology and Chemistry 29:2761-2768. http://dx.doi.org/10.1002/etc.327

López-Moreno, J.I., S. Fontaneda, J. Bazob, J. Revuelto, et al. 2014. Recent glacier retreat and climate trends in Cordillera Huaytapallana, Peru. Global and Planetary Change 112:1-11. http://dx.doi.org/10.1016/j.gloplacha.2013.10.010

Luebert, F., & M. Weigend. 2014. Phylogenetic insights into Andean plant diversification. Frontiers in Ecology and Evolution 2, Article 27, http://dx.doi.org/10.3389/fevo.2014.00027

Luteyn, J.L. 1999. Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature. New York Botanical Garden, Bronx.

MacDonald, G.M. 2010. Global warming and the Arctic: A new world beyond the reach of the Grinnellian niche? The Journal of Experimental Biology 213:855-861. http://dx.doi.org/10.1242/jeb.039511

MacDougall, A.H., C.A. Avis, & A.J. Weaver. 2012. Significant contribution to climate warming from the permafrost carbon feedback. Nature Geoscience 5:719-721. http://dx.doi.org/10.1038/ngeo1573

Mahlstein, I., R. Knutti, S. Solomon, & R.W. Portmann. 2011. Early onset of significant local warming in low latitude countries. Environmental Research Letters 6, 034009 http://dx.doi.org/10.1088/1748-9326/6/3/034009

Malanson, G.P., L.M. Resler, M.Y. Bader, F.-K. Holtmeier, D.R. Butler, D.J. Weiss, L.D. Daniels, & D.B. Fagreet. 2011. Mountain treelines: A roadmap for research orientation. Arctic, Antarctic, and Alpine Research 43:167-177. http://dx.doi.org/10.1657/1938-4246-43.2.167

Mark, B.G., J. Bury, J.M. McKenzie, A. French, & M. Baraer. 2010. Climate change and tropical Andean glacier recession: Evaluating hydrologic changes and livelihood vulnerability in the Cordillera Blanca, Peru. Annals of the Association of American Geographers 100:794-805. http://dx.doi.org/10.1080/00045608.2010.497369

Mark, B.G., & G.O. Seltzer. 2005. Evaluation of recent glacier recession in the Cordillera Blanca, Peru (AD 1962–1999): Spatial distribution of mass loss and climatic forcing. Quaternary Science Reviews 24: 2265-2280. http://dx.doi.org/10.1016/j.quascirev.2005.01.003

Mayer, E. 2002. The Articulated Peasant: Household Economies in the Andes. Westview Press, Boulder, CO.

Metcalfe, S.E., & D.J. Nash, eds. 2012. Quaternary Environmental Change in the Tropics. John Wiley, Chichester, West Sussex. http://dx.doi.org/10.1002/9781118336311

Monzón, J., L. Moyer-Horner, & M.B. Palamar. 2011. Climate change and species range dynamics in protected areas. Bioscience 61:752-761. http://dx.doi.org/10.1525/bio.2011.61.10.5

Mora, C., A.G. Frazier, R.J. Longman, R.S. Dacks, et al. 2013. The projected timing of climate departure from recent variability. Nature 502:183-187. http://dx.doi.org/10.1038/nature12540

Morgan, J.A., D.G. Milchunas, D.R. LeCain, M. West, & A.R. Mosier. 2007. Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. Proceedings of the National Academy of Science 104: 14724-14729. http://dx.doi.org/10.1073/pnas.0703427104

Mutke, J., R. Jacobs, K. Meyers, T. Henning, & M. Weigend. 2014. Diversity patterns of selected Andean plant groups correspond to topography and habitat dynamics, not orogeny. Frontiers in Genetics 5: Article 351; http://dx.doi.org/10.3389/gene.2014.00351

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, & J. Kent, 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858. http://dx.doi.org/10.1038/35002501

Naito, A.T., & D.M. Cairns. 2011. Patterns and processes of global shrub expansion. Progress in Physical Geography 35:423-442. http://dx.doi.org/10.1177/0309133311403538

Olson, D.M., E. Dinerstein, E.D. Wikramanayake, et al. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. Bioscience 51:933-938. http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Polley, H.W., H.B. Johnson, & H.S. Mayeux. 1994. Increasing CO2: Comparative responses of the C4 grass Schizachyrium and grassland invader Prosopis. Ecology 75:976-988. http://dx.doi.org/10.2307/1939421

Ponette-González, A.G., E. Marín-Spiotta, K.A. Brauman, K.A. Farley, K.C. Weathers, & K.R. Young. 2014. Hydrologic connectivity in the high-elevation tropics: Heterogeneous responses to land change. Bioscience 64:92-104. http://dx.doi.org/10.1093/biosci/bit013

Postigo, J.C. 2012. Responses of Plants, Pastoralists, and Governments to Social Environmental Changes in the Peruvian Southern Andes. Doctor of Philosophy Dissertation. University of Texas, Austin.

Postigo, J.C., M. Montoya, & K.R. Young. 2013. Natural resources in the subsoil and social conflicts on the surface: Perspectives on Peru's subsurface political ecology, in: A.J. Bebbington & J.T. Bury (eds.), Subterranean Struggles: New Geographies of Extractive Industries in Latin America. University of Texas Press, Austin, pp. 223-40.

Postigo, J.C., K.R. Young, & K.A. Crews. 2008. Change and continuity in a pastoralist community in the high Peruvian Andes. Human Ecology 36:535-551. http://dx.doi.org/10.1007/s10745-008-9186-1

Rabatel, A., B. Francou, A. Soruco, et al. 2013. Current state of glaciers in the tropical Andes: A multi-century perspective on glacier evolution and climate change. The Cryosphere 7:81-102. http://dx.doi.org/10.5194/tc-7-81-2013

Radić, V., & R. Hock. 2011. Regionally differentiated contribution of mountain glaciers and ice caps to future sea-level rise. Nature Geoscience 4:91-94 http://dx.doi.org/10.1038/ngeo1052

Ramírez, E., B. Francou, P. Ribstein, M. Descloitres, R. Guérin, J. Mendoza, R. Gallaire, B. Pouyaud, & E. Jordan. 2001. Small glaciers disappearing in the tropical Andes: A case study in Bolivia: Glaciar Chacaltaya (16°S). Journal of Glaciology 47:187-194. http://dx.doi.org/10.3189/172756501781832214

Rehm, E.M., & K.J. Feeley. 2013. Forest patches and the upward migration of timberline in the southern Peruvian Andes. Forest Ecology and Management 305: 204-211. http://dx.doi.org/10.1016/j.foreco.2013.05.041

Rodbell, D.T., G.O. Seltzer, B.G. Mark, J.A. Smith, & M.B. Abbott. 2008. Clastic sediment flux to tropical Andean lakes: records of glaciation and soil erosion. Quaternary Science Reviews 27:1612-1626. http://dx.doi.org/10.1016/j.quascirev.2008.06.004

Rodríguez, L.O., & K.R. Young. 2000. Biological diversity of Peru: Determining priority areas for conservation. Ambio 29:329-337. http://dx.doi.org/10.1579/0044-7447-29.6.329

Rundel, P.W., I.A. Dickie, & D.M. Richardson. 2014. Tree invasions into treeless areas: mechanisms and ecosystem processes. Biological Invasions, http://dx.doi.org/10.1007/s10530-013-0614-9

Rundel, P.W., A.P. Smith, & F.C. Meinzer. 1994. Tropical Alpine Environments: Plant Form and Function. Cambridge University Press, Cambridge. http://dx.doi.org/10.1017/CBO9780511551475

Schmidt, S.K., C.C. Cleveland, D.R. Nemergut, S.C. Reed, A.J. King, & P. Sowell. 2011. Estimating phosphorus availability for microbial growth in an emerging landscape. Geoderma 163:135-140. http://dx.doi.org/10.1016/j.geoderma.2011.04.014

Schmidt, S.K., C.S. Naff, & R.C. Lynch. 2012. Fungal communities at the edge: Ecological lessons from high alpine fungi. Fungal Ecology 5:443-452. http://dx.doi.org/10.1016/j.funeco.2011.10.005

Schmidt, S.K., D.R. Nemergut, J.L. Darcy, & R. Lynch. 2014. Do bacterial and fungal communities assemble differently during primary succession? Molecular Ecology 23:254-258. http://dx.doi.org/10.1111/mec.12589

Schmidt, S.K., D.R. Nemergut, A.E. Miller, K.R. Freeman, A.J. King, & A. Seimon. 2009. Microbial activity and diversity during extreme freeze–thaw cycles in periglacial soils, 5400 m elevation, Cordillera Vilcanota, Peru. Extremophiles 13:807-816. http://dx.doi.org/10.1007/s00792-009-0268-9

Schmidt, S.K., S.C. Reed, D.R. Nemergut, A.S. Grandy, C.C. Cleveland, M.N. Weintraub, A. W. Hill, E.K. Costello, A.F. Meyer, J.C. Neff, & A.M. Martin. 2008. The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils. Proceedings of the Royal Society B 275:2793-2802. http://dx.doi.org/10.1098/rspb.2008.0808

Sedan, R.E., & K.J. Burns. 2010. Are the northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). Journal of Biogeography 37:325-343. http://dx.doi.org/10.1111/j.1365-2699.2009.02200.x

Seimon, T.A., A. Seimon, P. Daszak, S.R.P. Halloy, et al. 2007. Upward range extension of Andean anurans and chytridiomycosis to extreme elevations in response to tropical deglaciation. Global Change Biology 13:288-299. http://dx.doi.org/10.1111/j.1365-2486.2006.01278.x

Sklenár, P., I. Hedberg and A.M. Cleef. 2014. Island biogeography of tropical alpine floras. Journal of Biogeography 41:287-297. http://dx.doi.org/10.1111/jbi.12212

Spehn, E.M., M. Liberman, & C. Körner (eds.). 2006. Land Use Change and Mountain Biodiversity. Taylor & Francis, Boca Raton. http://dx.doi.org/10.1201/9781420002874

Stansell, N.D., D.T. Rodbell, M.B. Abbott, & B.G. Mark. 2013. Proglacial lake sediment records of Holocene climate change in the western Cordillera of Peru. Quaternary Science Reviews 70:1-14. http://dx.doi.org/10.1016/j.quascirev.2013.03.003

Thompson, L.G., H.H. Brecher, E. Mosley-Thompson, D.R. Hardy, & B.G. Mark. 2009. Glacier loss on Kilimanjaro continues unabated. Proceedings of the National Academy of Science 106:19770-19775. http://dx.doi.org/10.1073/pnas.0906029106

Thompson, L.G., E. Mosley-Thompson, H. Brecher, M. Davis, B. León, D. Les, Ping-Nan Lin, T. Mashiotta, & K. Mountain. 2006. Abrupt tropical climate change: Past and present. Proceedings of the National Academy of Science 103:10536-10543. http://dx.doi.org/10.1073/pnas.0603900103

Thompson, L.G., E Mosley-Thompson, M.E. Davis, V.S. Zagorodnov, I.M. Howat, V.N. Mikhalenko, & P.-N. Lin. 2013. Annually resolved ice core records of tropical climate variability over the past ~1800 years. Science 340:945-950. http://dx.doi.org/10.1126/science.1234210

Tinoco, B.A., P.X. Astudillo, S.C. Latta, D. Strubbe, & C.H. Graham. 2013. Influence of patch factors and connectivity on the avifauna of fragmented Polylepis forest in the Ecuadorian Andes. Biotropica 45:602-611. http://dx.doi.org/10.1111/btp.12047

Tovar, C., C.A. Arnillas, F. Cuesta, & W. Buytaert. 2013. Diverging responses of tropical Andean biomes under future climate conditions. PLoS ONE 8, 5, e63634. doi:10.1371/journal.pone.0063634 http://dx.doi.org/10.1371/journal.pone.0063634

Tovar, C., J.F. Duivenvoorden, I. Sánchez-Vega, & A.C. Seijmonsbergen. 2012. Recent changes in patch characteristics and plant communities in the jalca grasslands of the Peruvian Andes. Biotropica 44:321-330. http://dx.doi.org/10.1111/j.1744-7429.2011.00820.x

Turner, M.G. 2005. Landscape ecology: What is the state of the science? Annual Review of Ecology and Systematics 36:319-344. http://dx.doi.org/10.1146/annurev.ecolsys.36.102003.152614

Urrutia, R., & M. Vuille. 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. Journal of Geophysical Research, 114, D02108, http://dx.doi.org/10.1029/2008JD011021

Valdivia, C., A. Seth, J.L. Gilles, M. García, E. Jiménez, J. Cusicanqui, F. Navia, & E. Yucra. 2010. Adapting to climate change in Andean ecosystems: Landscapes, capitals, and perceptions shaping rural livelihood strategies and linking knowledge systems, Annals of the Association of American Geographers 100:818-834. http://dx.doi.org/10.1080/00045608.2010.500198

Vuilleumier, F., & M. Monasterio, eds.1986. High Altitude Tropical Biogeography. Oxford University Press, Oxford.

Walker, L.R., & R. del Moral. 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, Cambridge. http://dx.doi.org/10.1017/CBO9780511615078

Walker, L.R., D.A. Wardle, R.D. Bardgett, & B.D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725-736. http://dx.doi.org/10.1111/j.1365-2745.2010.01664.x

Williams, J.W., S.T. Jackson, & J.E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences 104:5738-5742. http://dx.doi.org/10.1073/pnas.0606292104

Young, K.R. 1989. The tropical Andes as a morphoclimatic zone. Progress in Physical Geography 13:13-22. http://dx.doi.org/10.1177/030913338901300102

Young, K.R. 1993. National park protection in relation to the ecological zonation of a neighboring human community: An example from northern Peru. Mountain Research and Development 13:267-280. http://dx.doi.org/10.2307/3673656

Young, K.R. 1997. Wildlife conservation in the cultural landscapes of the central Andes. Landscape and Urban Planning 38:137-147. http://dx.doi.org/10.1016/S0169-2046(97)00029-7

Young, K.R. 1998. Deforestation in landscapes with humid forests in the central Andes: Patterns and processes, in: K.S. Zimmerer & K. R. Young (eds.), Nature's Geography: New Lessons for Conservation in Developing Countries. University of Wisconsin Press, Madison, pp. 75-99.

Young, K.R. 2008. Stasis and flux in long-inhabited locales: Change in rural Andean landscapes, in: A. Millington & W. Jepson (eds.), Land-Change Science in the Tropics: Changing Agricultural Landscapes. Springer, New York, pp. 11-32.

Young, K.R. 2009. Andean land use and biodiversity: Humanized landscapes in a time of change. Annals of the Missouri Botanical Garden 96:492-507. http://dx.doi.org/10.3417/2008035

Young, K.R. 2013. Change in tropical landscapes: Implications for health and livelihoods, in: B.H. King & K.A. Crews (eds.), Ecologies and Politics of Health. Routledge, New York, pp. 55-72.

Young, K.R., & P.L. Keating. 2001. Remnant forests of Volcán Cotacachi, northern Ecuador. Arctic, Antarctic, and Alpine Research 33:165-172. http://dx.doi.org/10.2307/1552217

Young, K.R., & B. León. 2007. Tree-line changes along the Andes: Implications of spatial patterns and dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 362:263-272. http://dx.doi.org/10.1098/rstb.2006.1986

Young, K.R., B. León, P.M. Jørgensen, & C. Ulloa Ulloa. 2007. Tropical and subtropical landscapes of the Andes Mountains, in: T. Veblen, K.R. Young, & A.R. Orme (eds.), The Physical Geography of South America. Oxford University Press, Oxford, pp. 200-216.

Young, K.R., & J.K. Lipton. 2006. Adaptive governance and climate change in the tropical highlands of western South America. Climatic Change 78:63-102. http://dx.doi.org/10.1007/s10584-006-9091-9

Young, K.R., C. Ulloa Ulloa, J.L. Luteyn, & S. Knapp. 2002. Plant evolution and endemism in Andean South America: An introduction. Botanical Review 68:4-21. http://dx.doi.org/10.1663/0006-8101(2002)068[0004:PEAEIA]2.0.CO;2

Zimmerer, K.S. 1991. Wetland production and smallholder persistence: Agricultural change in a highland Peruvian region. Annals of the Association of American Geographers 81:443-463. http://dx.doi.org/10.1111/j.1467-8306.1991.tb01704.x

Zimmerer, K.S. 1999. Overlapping patchworks of mountain agriculture in Peru and Bolivia: Toward a regional-global landscape model. Human Ecology 27:135-165. http://dx.doi.org/10.1023/A:1018761418477

Zimmermann, M., P. Meir, M.R. Silman, et al. 2010. No differences in soil carbon stocks across the tree line in the Peruvian Andes. Ecosystems 13:62-74. http://dx.doi.org/10.1007/s10021-009-9300-2